

PHYLOGENY OF THE AMERICAN GENERA OF SOLVIDAE
(XYLOMYIDAE) (DIPTERA), WITH ILLUSTRATIONS OF THE
FEMALE SPERMATHECA*

FILOGENIA DE LOS GENEROS AMERICANOS DE SOLVIDAE
(XYLOMYIDAE) (DIPTERA), CON ILUSTRACIONES DE LA
ESPERMOTECA DE LAS HEMBRAS

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ABSTRACT

A brief history of the taxonomy of the family Solvidae is given and a phylogeny presented for the three American genera: *Solva* (s.l.) is considered the sister-group of *Arthropeina* Lindner, and the ancestral species of both genera is considered as the sister-group of the ancestral species of *Macroceromys* Bigot. The female spermatheca offers valuable characters for the distinction of these three genera.

KEYWORDS America, Diptera, Solvidae, Xylomyidae, Phylogeny, Spermatheca.

RESUMEN

Se presenta una breve historia de la taxonomía de la familia Solvidae con una propuesta de filogenia de los tres géneros americanos: *Solva* (s.l.) se considera el grupo hermano de *Arthropeina* Lindner y la especie ancestral de esos dos géneros como el grupo hermano de la especie ancestral de *Macroceromys* Bigot. Las espermatecas de las hembras brindan valiosos caracteres para la distinción de los tres géneros.

PALABRAS CLAVES América, Diptera, Solvidae, Xylomyidae, Filogenia, Espermateca.

A BRIEF HISTORY OF THE TAXONOMY OF THE SOLVIDAE

In 1820 Meigen created the genus *Subula* to include some of the species he had previously described in *Xylophagus* (*varius*, *marginatus* and *maculatus*). *Xylophagus varius* was subsequently designated by Rondani (1856:172) as the type-species of *Subula* Meigen. This species has a two-segmented palpus, the hind femur is more or less elongated and cylindrical and bears no denticles on its ventral surface, the first abdominal tergite has a very wide membranous area, M₂ ends

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before the wing margin, C ends in M_1 , the transverse crossvein m-cu is present, and the antenna has elongated flagellomeres (cf. Hennig, 1967: figs. 20 (wing), 24 (abdominal tergites 1 and 2 and hind leg), 30 (antenna)).

Walker (1859) erected *Solva* for his Oriental species *inamoena*; *Solva* has an incrassate hind femur bearing a row of denticles on its ventral surface.

As *Subula* Meigen was preoccupied (*Subula*. Schumacher, 1817), Rondani rebaptized it as *Xylomya*; the type-species is, therefore, *Xylophagus varius* Meigen (automatically). Apparently unaware of this fact, Williston also proposed a new name for *Subula* Meigen-*Subulaomyia*.

Bigot (1877) described the first American representative of this group-*Macroceromys* (type-species, *fulviventris* Bigot, mon.; from Mexico). This species has very slender and elongate hind femora without denticles on the ventral surface, the first abdominal tergite has a very narrow membranous area, elongated antennal flagellum and a one-segmented palpus.

Enderlein (1913) started the confusion within this group of flies. He wrongly designated *Xylophagus maculatus* Meigen as the type-species of *Xylomya* Rondani; he erected two genera more, *Prista* (Oriental) and *Subulonia* (Neotropical), related to *Solva* Walker; he ignored *Macroceromys* Bigot. He distinguished those genera by the following key (slightly modified):

- “1. m_3 und cu_1 nahe der Basis durch Querader verbunden [i.e., crossvein m-cu present] 2
- m_3 und cu_1 nahe der Basis eine Strecke weit verschmolzen (Mediocubitalquerader fehlt).
Fühler 10 gliedrig, normal. m_3 nicht verkürzt. (Hinterschenkel etwas verdickt, verbreitert un längs des unteren Randes fein gezähnel) *Prista* Enderlein
- 2(1). 3. Fühlerglied besonders verdickt und gross; 4.-10. Glied stark verkürzt (quer). (m_3 mehr oder weniger stark verkürzt. Hinterschenkel etwas verbreitert, verdickt und längs des unteren Randes mit feiner körniger Zähnelung)*Subulonia* Enderlein
3. Fühlerglied wohl länger als die übrige, aber niemals gross und dick; 4.-6. Glied nicht quer. m_3 nicht verkürzt 3
- 3(2). Interschenkel nicht verdickt und ohne Zähnelung“*Xylomya*”
Hinterschenkel etwas verbreitert und verdickt un längs des unteren Randes mit feiner körniger Zähnelung*Solva* Walker”

Let it be noticed that in Enderlein’s key “*Xylomya*” corresponds to *Macroceromys* Bigot, as can be seen by the characters given. Moreover, *Xylophagus maculatus* Meigen, which was erroneously fixed by Enderlein as the type-species of *Xylomya sensu* Enderlein is clearly a *Macroceromys* (cf. Hennig, 1967: figs. 18 (wing), 22 (abdominal tergites 1 and 2 and hind leg), 27 (antenna)). From the on, “*Xylomya*” (we are going to indicate this concept by *Xylomya sensu* Enderlein) would be used by all subsequent authors in the meaning of *Macroceromys* Bigot.

Meijere (1914) erected the genus *Ceratosolva* (type-species, *cylindricornis* Meijere, Oriental). This genus is curiously “intermediary” between *Xylomya* Rondani (like this *Ceratosolva* has a slender, cylindrical hind femur) and *Solva* Walker (*Ceratosolva* has ventral denticles on the ventral surface of the hind femur, but is not incrassate as in *Solva*); in addition, it has m-cu present and the antennal flagellum is elongate.

Enderlein (1920) described *Hanauia* (for *Xylophagus marginatus* Meigen); like *Solva*, this species has an incrassate hind femur with a row

of denticles on the ventral surface; m-cu, in *Hanaia*, is reduced to a mere point.

Brunetti (1920) created *Pararthropeas* (type-species, *thereviformis* Brunetti, Oriental), also apparently related to *Solva* Walker (i.e., hind femur incrassate, with denticles on the ventral surface).

Pleske (1925) described, from the Palaearctic, the genus *Nematoceropsis* (type-species, *ibex* Pleske), apparently related (or the same as?) to *Macroceromys* Bigot.

James (1939) erected the subgenus *Formosolva* (of *Solva*) (type-species, *concaivfrons* James, Oriental), declaring that it can "be distinguished from *Ceratosolva* [Meijere] by the longer antenna, the broad, concave front and the

long first antennal segment". *Formosolva* has, like *Ceratosolva*, a more or less slender and elongate hind femur with a series of denticles on the ventral surface, and m-cu is present.

Hull (1944) added to *Solva* the subgenus *Phloophila* (type-species, *pallipes* Loew, Nearctic); it has the hind femur incrassate, with ventral denticles (therefore belonging to the *Solva*-group); m-cu is reduced to a point (differing in this aspect from *Subulonia* Enderlein, which has a distinct m-cu).

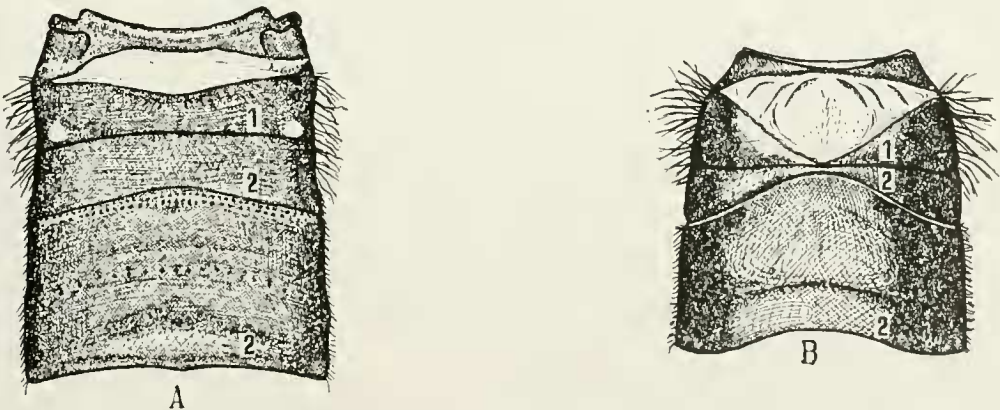
Steyskal (1947) revised the Nearctic species of Solvidae, accepting only two genera, and introduced some interesting new morphological characters, as can be seen in his key:

"Hind femora swollen and furnished beneath with minute teeth, flagellum of antennae with the joints distinctly although but slightly separated, the terminal joint twice as long as the preceding one, with a short but distinct conical bare shining tip, the first joint sometimes considerably enlarged; the second abdominal tergite membranous medianly except the posterior margin, allowing itself to fit closely to the metanotum when the abdomen is greatly upflexed; wings with at least one branch of the media not reaching margin, crossvein m-cu short or absent; all veins microsetate above*Solva* Walker.

Hind femora not markedly thicker than the others and lacking teeth below; flagellum with the joints apparently fused, the first joint never enlarged; the second abdominal tergite not membranous anteromedianly; wing with all branches of media strong and reaching margin, crossvein m-cu well developed; wing veins posterior to radius not microsetate*Xylomya*"

What Steyskal called 'Xylomya' (because he accepted Enderlein's fixation of *Xylophagus maculatus* Meigen as the type-species) is

undoubtedly *Macroceromys* Bigot. It should be noticed that the membranous area is situated on tergite 1 (and not 2 as in the key) (Textfig.1).



TEXTFIG. 1. Abdominal tergites 1-2, ♀. A. *Macroceromys moiwana* (Matsumura); B. *Solva procera* (Frey). 1: Tergite 1; 2. Tergite 2. (apud Nagatomi & Tanaka. 1971).

Steyskal placed *Subulonia* Enderlein, 1913, *Hanauia* Enderlein, 1913, and *Phoophila* Hull, 1944, in the synonymy of *Solva* Walker, 1859.

Frey (1960) recognized three groups of species within the family Solvidae:

1. Hind femur cylindrical, without denticles on the ventral surface - 'Xylomya' (i.e., *Macroceromys* Bigot; *Nematoceropsis* Pleske was synonymized here);
2. Hind femur incrassate, with denticles on the ventral surface - *Solva* Walker;
3. Hind femur cylindrical, with denticles below - *Ceratosolva* Meijere.

THE CONTRIBUTION OF NAGATOMI & TANAKA (1971)

A major advance in the knowledge of the Solvidae as contributed by Nagatomi & Tanaka (1971), in their revision of the Japanese species. The two authors accepted as valid the genera *Arthropaina* Lindner (1949; this genus differs from all other genera in the shape of the antennal flagellum; Lindner described it from the Neotropics; type-species, *fulva* Lindner), *Cenomyiodes* Brunetti (we doubt this genus belongs here) and *Solva* Walker, with two "subgenera"- *Solva* proper and *Macroceromys* Bigot. Nagatomi & Tanaka included in the synonymy of *Solva* s.s. the genera *Xylomya* Rondani, *Subulonia* Enderlein,

Prista Enderlein, *Ceratosolva* Meijere, *Pararthropeas* Brunetti, *Hanauia* Enderlein, and the subgenera *Formosolva* James and *Phloophila* Hull; *Nematoceropsis* Pleske was considered a synonym of *Macroceromys* Bigot.

The best contribution of Nagatomi & Tanaka is the careful study of the male terminalia of the Japanese species; the terminalia affords many important and clearcut characters for the separation of the species. This can be resumed in the following manner (we are reinterpreting here some of the original data; numbers of figures cited in parentheses refer, of course, to Nagatomi & Tanaka's 1971 paper):

1. Hypandrium present, its mid-anterior margin deeply concave, free from base of basistyli (4E) or fused to bases of basistyli (3E, 5E, 6E, 7E, 9B). Epandrium with a pair of laterodistal processes (3E, 4F, 5F, 6F, 7F, 9C). Aedeagus large (3D, 4D, 5D, 6D, 7D, 9D). Dististylus large and broad, its base more or less constricted (3D, 4D, 5D, 6D, 7D, 9A). "Interbases" present (3D, 4D, 5D, 6D, 7D, 8A). Sternite 8 with a pair of apical flat processes (3G, 4G, 5G, 6G, 7G, 9D) *Macroceromys* Bigot.
- Hypandrium absent* (12E, 13E, 14E, 15F). Epandrium without a pair of laterodistal processes (12F, 13F, 14F, 15G) 2
- 2(1). "Interbases" absent (12D, 13D, 14D-E). Sternite 8 without a pair of apical flat processes. Dististylus present (12D-E, 13D-E, 14D-E). (*Antennal flagellum shortened. Hind femur incrassate, with denticles on ventral surface*) *Solva*, group 1.
- "Interbases" present, very large (long and broad) (15E-F). Sternite 8 with a pair of apical flat processes (15H). Dististylus absent (15E). Aedeagus small. Antennal flagellum elongate. *Hind femur incrassate*, but with very small denticles beneath, "which may be overlooked" *Solva*, group 2.

Characters in *italics* represent, according to us, apomorphic characters (polarized by outgroup comparison, the outgroup being all the other Brachycera).

It is interesting to note that the presence of a pair of apical flat processes on sternite 8 is probably homoplastic, having independently evolved in *Macroceromys* and group 2 (*Solva procera* (Frey)) of *Solva*. It becomes manifest, from the above list of characters, that at least three sound (phylogenetic) groups of species (let's say genera) exist in Japan.

The same should be made for the rest of the Solvidae in the world. Dissections of male terminalia are needed, to decide on the validity of the nominal genera and subgenera thus far proposed. It is very likely that many of them will prove to be valid concepts, or that new genera may be needed.

To resume the present situation within the Solvidae, we may say that this family can be divided in the following manner (pointing out at the same time the open taxonomic problems):

1. A group of species with tergite 1 with a small, reduced membranous area; palpus with only one segment; hind femur cylindrical, elongate, without denticles on the ventral surface - *Macroceromys* Bigot (? = *Nematoceropsis* Pleske; the latter should be better studied in order to show whether it really belongs to the Solvidae and, in the affirmative case, whether it is distinct or not from *Macroceromys*).
2. A group of species with very large membranous area on tergite 1; palpus two-segmented:
 - 2.1. Basal 6 antennal flagellomeres fused, 8th flagellomere elongate; hind femur cylindrical, without ventral row of denticles - *Arthropeina* Lindner;
 - 2.2. Antennal flagellum never as above; other combinations of characters:
 - 2.2.1. Hind femur cylindrical, elongate, without denticles on ventral surface; m-cu present - *Xylomya* Rondani (with *Xylophagus varius* Meigen as type-species);
 - 2.2.2. Hind femur cylindrical, more or less elongate, with denticles on ventral surface; m-cu present - *Ceratosolva* Meijere and *Formosolva* James;
 - 2.2.3. Hind femur incrassate, with denticles on ventral surface; m-cu variable - *Solva* Walker, *Subulonia* Enderlein, *Prista* Enderlein, *Hanauia* Enderlein, *Pararthropeas* Brunetti, *Phloophila* Hull and *Solva procera* (Frey).

Notice that *Xylomya* Rondani is entirely based on plesiomorphic characters. Only dissections of male terminalia and female spermathecae could help to clarify the situation above.

spermathecae showed some very beautiful characters, which help extraordinarily well in the construction of the phylogeny. Our hypothesis is shown in Textfig. 2.

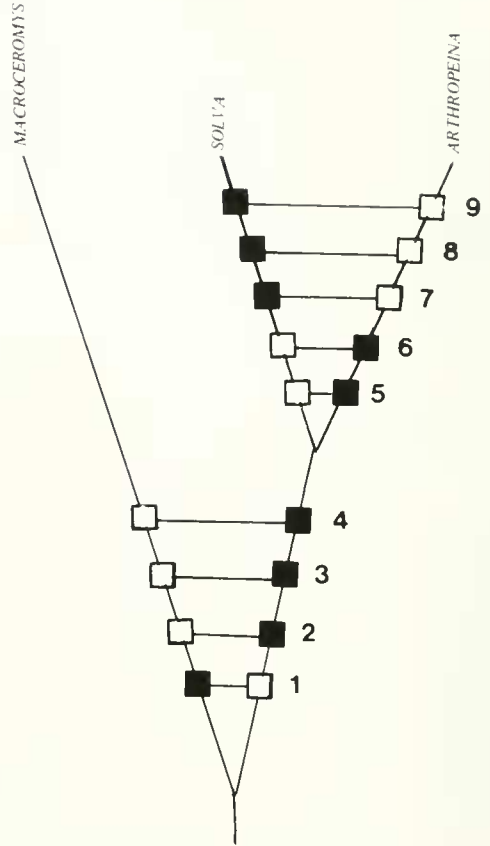
PHYLOGENY OF THE AMERICAN GENERA

We are considering here the groups *Macroceromys* Bigot, *Arthropeina* Lindner and *Solva* authors. Dissection of the female

The characters employed in the phylogenetic reconstruction are the following (characters in *italics* are in the apomorphic condition; polarization was made taking the remaining groups of Brachycera as the outgroup):

1. Palpus two-segmented (*Palpus one-segmented*)
2. Tergite 1 without membranous area or, if membranous area present, very small (*Tergite 1 with very large membranous area, almost reaching margin of tergite 1*)
3. Three spermathecae present (*Two spermathecae present*).
4. C present beyond M_1 (*C absent beyond M_1*)
5. Antennal flagellomere clearly separated (*Basal 6 antennal flagellomeres fused, 8th elongate*)
6. Spermathecal capsule not showing layers (*Spermathecal capsule 3-layered*)
7. Remnant of middle spermathecal duct present (*No vestige of duct of middle spermatheca*)
8. Crossvein m-cu present (*Crossvein m-cu absent*).

Most unfortunately, the male terminalia of the American "Solva" and *Arthropeina* are not known (there are no males in the collections seen); in the future they may add valuable characters for the phylogeny.



TEXTFIG. 2. Hypothetical phylogeny of the American groups of Solvidae.

KEY TO THE AMERICAN GROUPS OF SOLVIDAE

1. Palpus one- segmented. Membranous area at base of tergite 1 not evident or ending far away from posterior margin of that tergite (cf. Hennig, 1967: figs. 22-23 (p. 19)). Hind femur long and slender, narrower than hind coxa and without a series of denticles on ventral surface. Crossvein m-cu present. Costa ending in M_2 or M_1 . Three spermathecae present, the lateral ones with a long duct (reaching first abdominal segment and then bending backwards to segment 5) and more or less ovoid capsules, the median one with a very short duct and an exceedingly voluminous capsule (twice or more volume of lateral ones) (Figs. 1-4). Male with hypandrium present *Macroceromys* Bigot
- Palpus one- segmented. Abdominal tergite 1 with a more or less large, semicircular, basal, membranous (the integument very thin and transparent), anteriorly concave, pale area, which extends almost to the posterior margin of that tergite (cf. Hennig, 1967:figs. 24-25 (p. 19)). Posterior femur either slender or incrassate, either with or without denticles on ventral surface. Costa ending in M_1 . Crossvein m-cu either present or absent. Only two

- spermathecae present, the central one either absent or reduced to a short, whip-like filament (Figs. 6, 9) 2
- 2(1). Antennal flagellum with 8 distinct flagellomeres, which become gradually narrower towards apex. Hind femur incrassate, almost as wide as hind coxa, with a row of small, short denticles on ventral surface, except in the immediate basal portion. Crossvein m-cu absent. Central spermatheca totally absent, not even vestige of duct left, the lateral spermathecae with an extremely long duct, which performs seven and a half bends inside the abdomen (Figs. 5-7). Male terminalia with hypandrium absent
 *Solva*, authors (American species)
- Antennal flagellum with the basal 6 flagellomeres fused, spindle-shaped, the 7th flagellomere short but evident, the 8th greatly elongate, almost as long as the basal six flagellomere together. Hind femur slender and without ventral row of denticles. Crossvein m-cu present. Spermathecae: only the lateral ones present, the ducts moderately long, coiled; the central spermatheca represented only by a short, whip-like remnant of the duct (figs. 8-9). Male terminalia unknown *Arthropeina* Lindner

CATALOGUE OF NEOTROPICAL SOLVIDAE
(XYLOMYIDAE)Genus *Solva* Walker, *sensu lato*Genus *Arthropeina* Lindner

- Arthropeina* Lindner, 1949: 189. Type-species, *fulva* Lindner (mon.).
- fulva* Lindner, 1949: 789, fig. 3 (antenna). Type-locality: not stated (but undoubtedly Brazil, Santa Catarina, Nova Teutônia). Ref.- Lindner, 1969.

Genus *Macroceromys* Bigot

- Macroceromys* Bigot, 1877: lxxiii. Type-species, *fulviventris* Bigot (mon.).
- Xylomya*, authors, not Rondani.

- americanus* (Wiedemann), 1821a: 1 (1821b: 51) (*Xylophagus*). Type-locality: "North America". Distr.- Wyoming to Quebec, s. to Texas and Mississippi; Mexico. *N. COMB.*
- elongatus* (Osten Sacken), 1886: 62 (*Subula*). Type-locality: Guatemala, Capetillo. Distr.- Guatemala. *N. COMB.*
- fulviventris* Bigot, 1879: 187. Type-locality: "Mexico". Distr.- Mexico.
- fulviventris* Bigot, 1877: lxxiii (*nomen nudum*).
- prista* (Enderlein), 1913: 541 (*Xylomyia*). Type-locality: Mexico, Chiapas. Distr.- Mexico (Chiapas). *N. COMB.*

- ?*Subula* Meigen, 1820: 15 (preocc. Schumacher, 1817). Type-species, *Xylophagus varius* Meigen (Rondani 1856: 172) (Palearctic).
- Solva* Walker, 1859: 98. Type-species, *inamoena* Walker (mon.) (Oriental).
- ?*Xylomya* Rondani, 1861: 11 (nom. nov. for *Subula* Meigen). Type-species, *Xylophagus varius* Meigen (aut.).
- ?*Subulaomyia* Williston, 1896: 43 (as *Subula Omyia*) (nom. nov. for *Subula* Meigen, but deleted in Corrigenda, p. iv). Type-species, *Xylophagus varius* Meigen (aut.).
- ?*Subulonia* Enderlein, 1913: 545. Type-species, *truncativena* Enderlein (orig. des.) (Neotropical).
- ?*Prista* Enderlein, 1913: 546. Type-species, *Subula vittata* Doleschall (orig. des.) = *vittipes* Bezzi (Oriental).
- ?*Ceratosolva* Meijere, 1914: 21. Type-species, *cylindricornis* Meijere (mon.) (Oriental).
- ?*Hanauia* Enderlein, in Brohmer, 1920: 281. Type-species, *Xylophagus marginatus* Meigen (Enderlein, 1921c: 170) (Palearctic).
- ?*Pararthropeas* Brunetti, 1920: 108. Type-species, *thereviformis* Brunetti (orig. des.) (Oriental).
- ?*Solva* subg. *Formosolva* James, 1939: 32. Type-

- species, *conconvifrons* James (orig. des.) (Oriental).
- ?*Solva*, subg. *Phloophila* Hull, 1944: 263. Type-species, *Subula pallipes* Loew (orig. des.) (Nearctic).
- ?*brasiliana* (Lindner), 1949: 791 (*Subulonia*). Type-locality: Brazil, Santa Catarina, Nova Teutônia.
- ?*flavicoxis* (Enderlein), 1921: 172 (*Hanauia*). Type-locality: Paraguay, San Bernardino.
- ?*pallipes* (Loew), 1863: 6 (Centuria 3, n° 9) (*Subula*). Type-locality: USA, Illinois, Wisconsin. Distr.- USA, Canada, “?Middle America”.
- ?*truncativena* (Enderlein), 1913: 545 (*Subulonia*). Type-locality: Costa Rica.

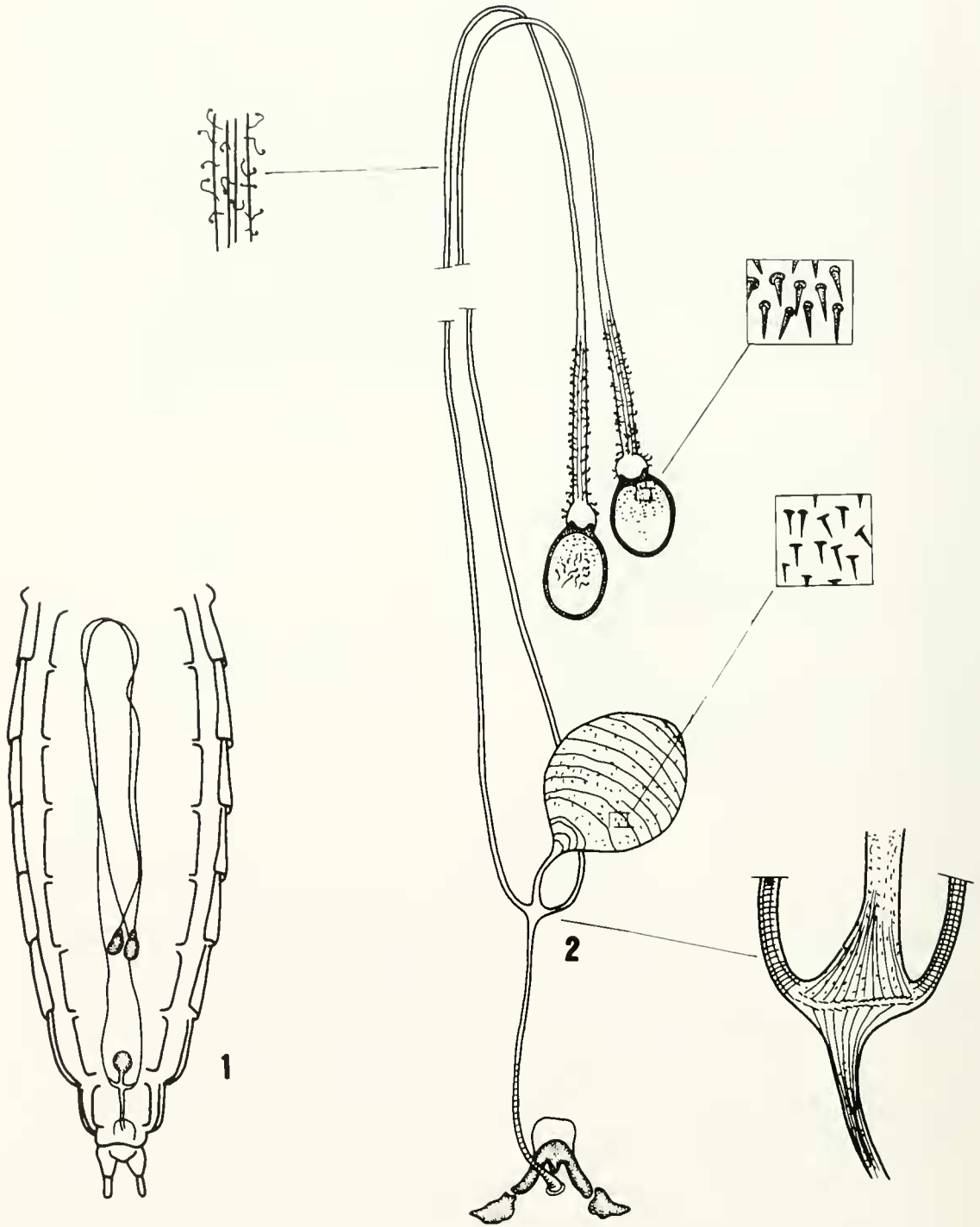
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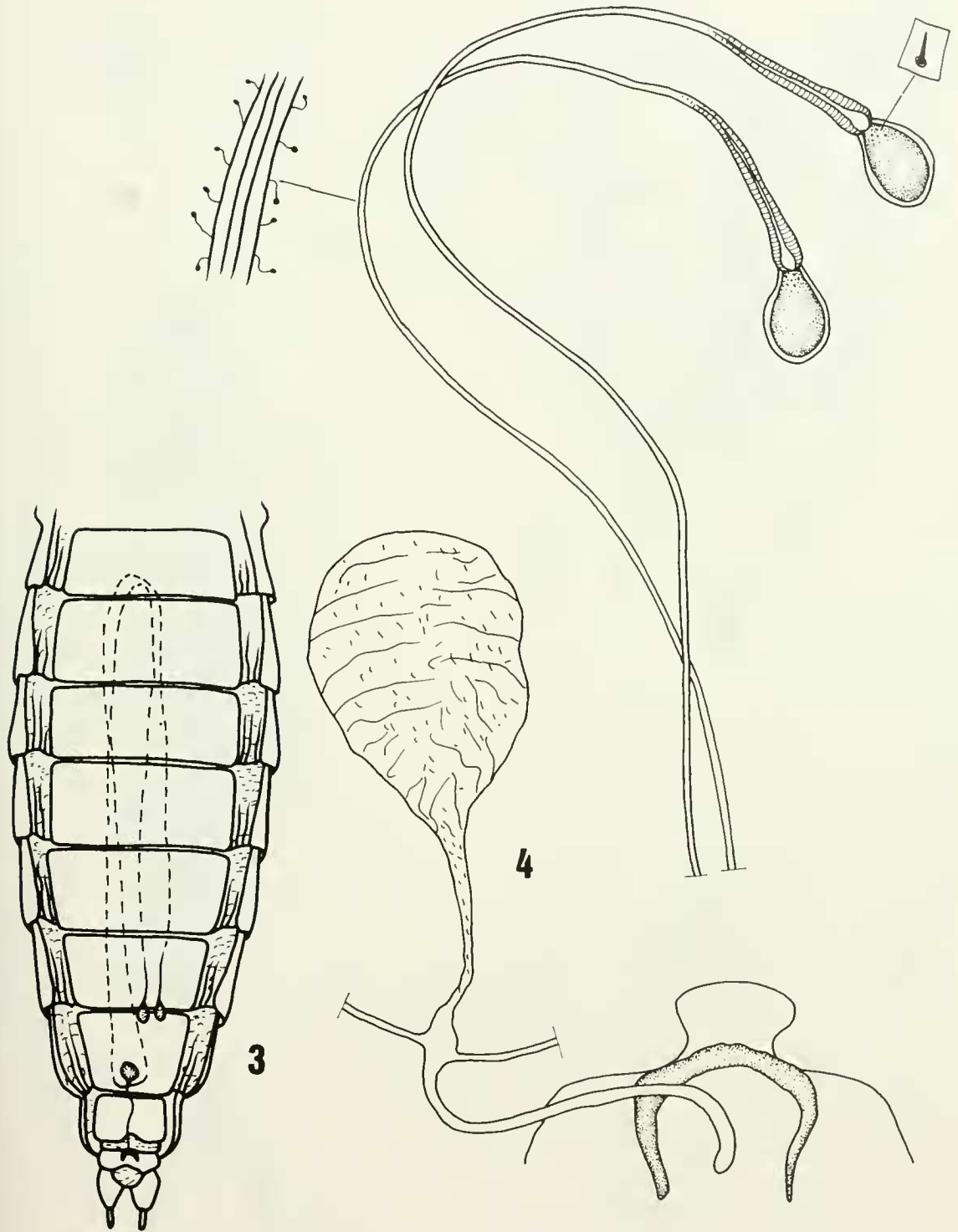
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(Synonyms in italics)

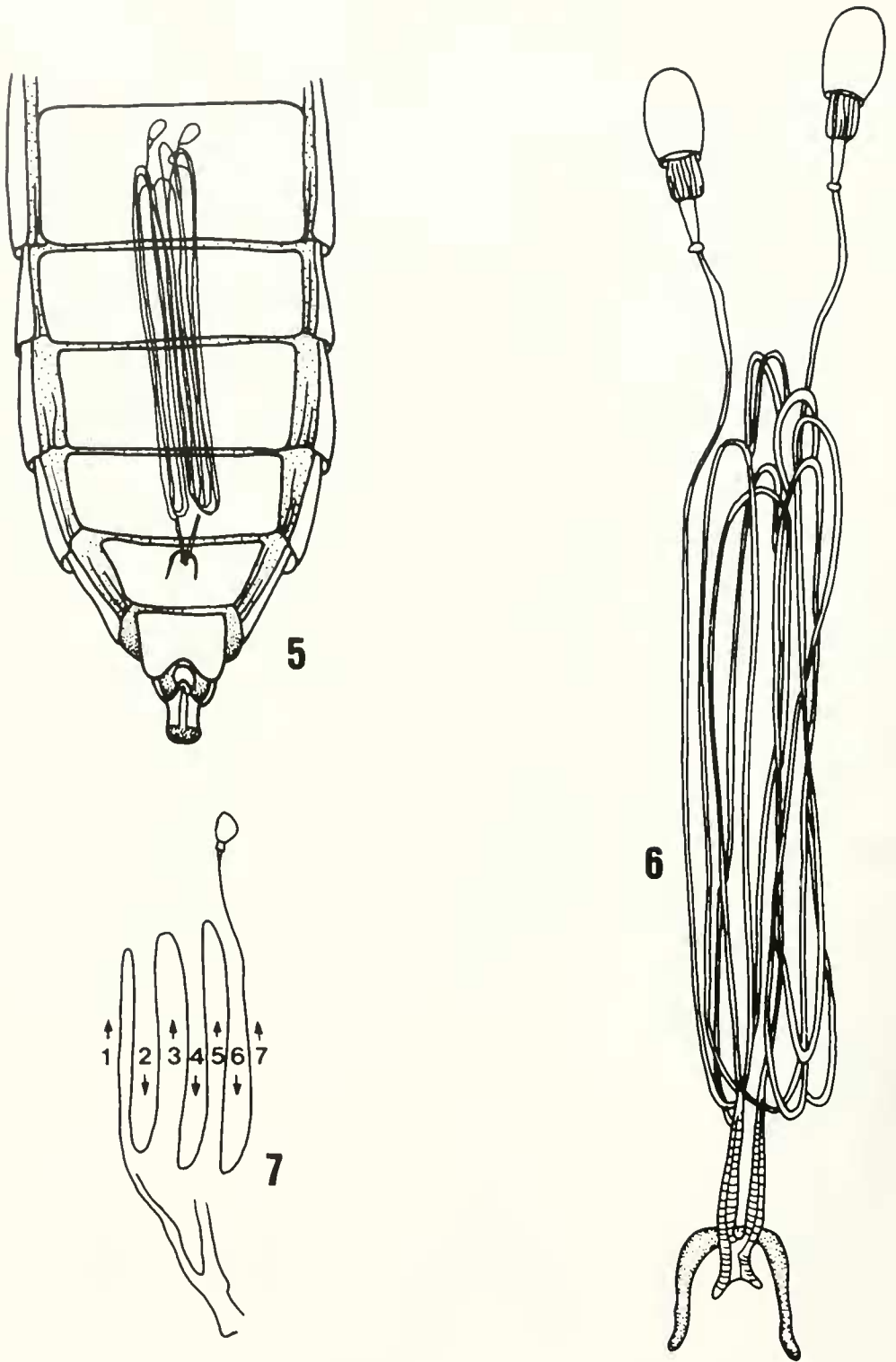
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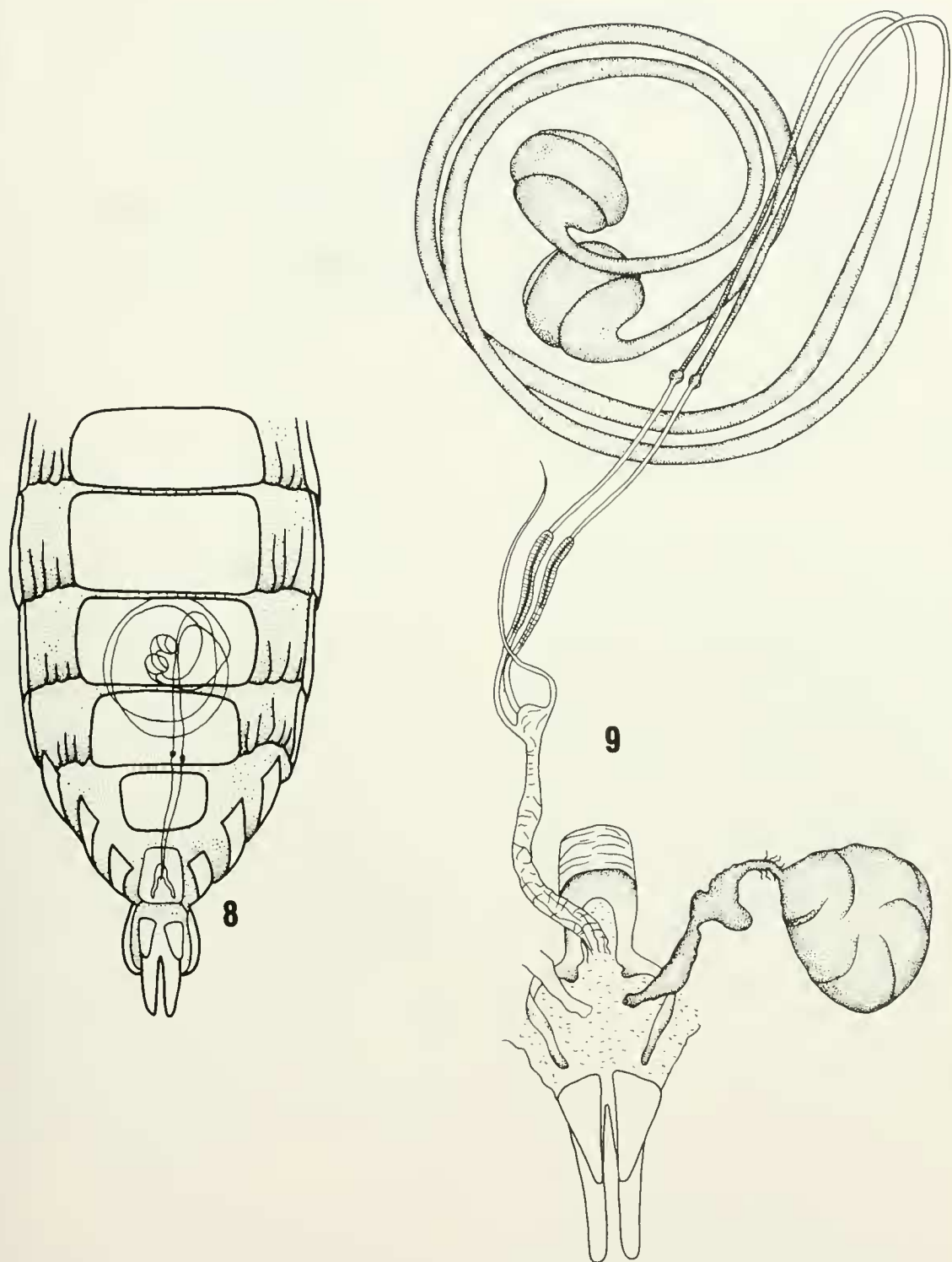
FIGS. 1-2. *Macroceromys pallidifemur* (Malloch); 1. Situation of the spermathecae in the abdomen; 2. Spermathecae and details.



FIGS. 3-4. *Macroceromys simillimus* (Steyskal): 3. Situation of the spermathecae in the abdomen; 4. Spermathecae and details.



FIGS. 5-7. *Solva* sp.: 5. Situation of the spermathecae in the abdomen; 6. Diagram showing the seven and a half loops a spermathecal duct; 7. Spermathecae.



FIGS. 8-9. *Arthropeina fulva* Lindner: 8. Situation of the spermathecae in the abdomen; 9. Spermathecae and accessory gland.